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The Sperm Transfer System in *Kinbergonuphis simoni* (Polychaeta:Onuphidae)

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Abstract. Tube dwelling *Kinbergonuphis simoni* (Santos, Day and Rice) achieves a 98.9% fertilization efficiency by means of a sperm transfer system involving spermatophores and seminal receptacles. The spermatophores are mushroom-shaped structures released as clumps. The seminal receptacles are paired sac-like organs embedded in the dorsal epidermis of female genital segments. Males release spermatophores into the environment, and females pick them up with their ventral palps and first pair of parapodia. Stored sperm remain viable for fertilization for at least one month. Spermatophore release and egg laying are independent of the presence of the opposite sex. Advantages associated with this system are discussed, and include asynchronous reproduction, a long breeding season, reduced sperm loss, and reduced exposure to risks. This sperm transfer mode is the first reported in the family Onuphidae and is proposed for other small, tube-dwelling onuphids.

Introduction

Sperm transfer in polychaetes occurs in two main modes: non-aggregate transfer, in which sperm are free swimming and not packed together before reaching eggs; and aggregate transfer, in which sperm are packed together by varying complex structures before reaching eggs.

Of the non-aggregate transfer modes, three different types have been recorded: broadcast spawning (Clark, 1961; Schroeder and Hermans, 1975), copulation (Just, 1914; Gray, 1969; Schroeder and Hermans, 1975; Westheide, 1984), and pseudocopulation (Reish, 1957; Pettibone, 1963; Daly, 1973). Three types of aggregate transfer have been recognized: indirect hypodermic impregnation, free transfer of spermatophores, and free transfer of spermatozeugmata. Among these three types, spermatozeugmata transfer (Austin, 1963; Eckelbarger, 1974) has not been elucidated with certainty, and will not be discussed further here.

In hypodermic impregnation, males actively place spermatophores on the body surface of females. Sperm may then be collected into seminal receptacles, or may penetrate through the epidermis into the coelom of females (Ax, 1968; Jouin, 1970; Westheide, 1984). In free transfer, the spermatophores are released into the environment and later picked up by females. Seminal receptacles are often noted. Free spermatophore transfer has been well demonstrated in members of the spionid genus *Polydora* (Rice, 1978a, 1987a), and has been strongly suggested to occur in serpulids and sabellids (Daly and Golding, 1977; Picard, 1980). The members of these three Families are tube dwellers.

Life history characteristics and habitat choice have been considered strong selective forces for the mode of sperm transfer (Rice, 1978a; Clark, 1981; Mann, 1984; Westheide, 1984). For example, sessile or tube dwelling life styles limit direct bodily contact, or decrease the mobility of individuals so that encounters between sexes are infrequent or impossible; thus, neither copulation, pseudocopulation, nor indirect hypodermic impregnation would be favored. Broadcast spawning or free transfer of spermatophores may be the only alternative for such species. However, broadcast spawning requires large numbers of gametes and synchronous reproduction in the population. The disadvantages of broadcast spawning have been reported (*e.g.*, in corals, Harrison *et al.*, 1984; Shlesinger and Loya, 1985; and in sea urchins, Pennington, 1985). In contrast, free spermatophore transfer with sperm storage, as found in the spionid *Poly-*

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dora, has been proposed as an efficient low risk mode of sexual reproduction (Rice, 1978a). Liberation of spermatophores into the sea also has been considered as an adaptive character in sessile tubicolous pogonophorans (Flügel, 1977) and vermetid gastropods (Hadfield and Hopper, 1980). Recently, a high efficiency of fertilization has been recorded in bivalves with similar free spermatophore transfer (Ó Foighil, 1985).

Reproduction in the Onuphidae has been reviewed in general, and developmental patterns have been studied in a few species (Blake, 1975; Fauchald, 1983; Paxton, 1986; Hsieh and Simon, 1987). However, no studies have been done on sperm transfer modes in this group. The characteristics of life style and life history of *Kinbergonuphis simoni* are similar to those of many *Polydora* species. Both are dioecious tube dwellers and are small in size. Females produce few, large yolky eggs, brood their young in the tubes, and have an extended breeding season (Rice, 1978a, b; Hsieh and Simon, 1987; Hsieh and Simon, unpub. data).

The goals of this study are to address: (1) the mode of sperm transfer in *Kinbergonuphis simoni;* (2) the fertilization efficiency of this mode; and (3) the possibility that the mode represents convergent evolution between spionids and onuphids.

Materials and Methods

Seminal receptacles

Worms were collected from an intertidal sandy flat in Upper Tampa Bay, Florida, and brought alive into the laboratory in January 1985. The presence of seminal receptacles was determined as follows: Two treatments—control and isolation—were set up. Five replicates were used as controls. In each replicate, a pair of male and female worms were reared in a plastic dish surrounded by mesh cloth to keep adults and juveniles from escaping. In the isolation experiment, seven females were separately incubated in the same way. Three of the seven females were brooding when experiments began. The females were tapped out of their tubes and thus separated from their young. These young were at embryonic or segmented stages. Seawater, which had been sealed in jars for four months, was filtered through Whatman No. 1 filter paper before being added to the aquaria. Salinity and temperature were maintained at 22‰ and 20°C, respectively. The presence of larvae and juveniles was noted at one- or two-week intervals. This study was conducted for three months.

Spermatophores

Mature worms were collected in March 1988 to determine the occurrence of spermatophores. In the laboratory, males were reared in mesh-enclosed dishes with and without females. Salinity was kept at 22–24‰, and temperature at 20–22°C. Observations on behavior and spermatophore production were made at intervals of 2 to 3 h during daylight hours for three weeks. In all laboratory experiments, the worms were fed ground alfafa.

Seminal receptacles and spermatophores: morphology

Mature females collected in May 1985, were prepared for paraffin sections after being fixed in Bouin's fixative. Subsequently, they were cut into 7- to 10-μm sections and stained in Ehrlich's hematoxylin and eosin (Knudsen, 1966). Spermatophores were prepared for SEM studies following the procedures of Hsieh and Simon (1987).

Fertilization efficiency

Worms were collected at the study site monthly in 1982, and from June to October in 1985, to determine the fertilization efficiency. Worms were relaxed in 0.15% propylene phenoxytol and fixed in 10% formalin in the field. Broods were examined in the laboratory. Unfertilized eggs could be recognized by a white coloration and a clear space appearing at one end (Fig. 1). Only the broods at early developmental stages (blastula to 5-setiger stages) were used to avoid underestimating the number of unfertilized eggs due to disintegration. Fertilization efficiency was expressed as the percentage of eggs fertilized of all eggs spawned.

Results

Seminal receptacles

Table I shows that, over three months, paired females produced one to three normally developing broods. Isolated females also laid eggs, suggesting that spawning was not induced by the presence of males. In some isolated females (No. 3, 4, and 6), eggs were present in maternal tubes, but no development was observed. In four of the seven isolated females, each produced only one viable brood, indicating that females did store sperm, but that the amount was insufficient for subsequent broods. In isolated females, 0 to 7 juveniles were produced, while in control pairs 9 to 64 offspring were produced (Table I).

Spermatophores

Spermatophores were released from male tube openings as clumps, which stuck to the bottom of the culture dishes or to pieces of debris. Occasionally, in clean dishes where no food particles were present, spermatophores were trapped in the water surface film. Freshly released spermatophores were white, almost transparent, very

Table I

Comparison of breeding success between isolated females and paired males and females of Kinbergonuphis simoni *reared in the laboratory from January to March, 1985*

Treatment	Date (1985) Jan 27	Feb 3	10	17	24	Mar 3	9	Number of viable broods produced	Number of juveniles produced
Control pairs									
1	*	J, 3		*	*	*	J, 6, *	2	9
2	J, 27	*	*	J, 9	*	*	J, 28	3	64
3	*	*	*	*	J, 17			1	17
4	J, 18	*	*	J, 16, *	*	*	J, 8	3	42
5	J, 5	*	*	*	J, 7			2	12
Isolated females									
1	*	J, 2						1	2
2		*	*	*	J, 4			1	4
3		*	*	*	*			0	0
4		*	*	*	*			0	0
5 brooder	*	J, 3						1	3
6 brooder		*	*	*	*			0	0
7 brooder	*	J, 7						1	7

* Larvae or eggs present in maternal tubes; J = juveniles present in dishes; numerals following J = brood sizes.

sticky, and easily broken when handled. Motile sperm were observed inside the intact spermatophores. The thin mucous sheets to which the spermatophores were attached were quickly broken down by ciliates or rotifers; however, the spermatophores themselves remained intact for more than 48 h.

Spermatophores produced at one time by individual males could form more than one clump. The number of spermatophores in each clump varied, ranging from 33 to 160 (mean ± 1 S.E. = 84.90 ± 12.66, n = 10). The average number of spermatophores produced by an individual male at one time was 80.25 ± 18.26 (n = 4). Spermatophores were present in all of the culture dishes, with or without females, indicating that production of spermatophores was not influenced by the presence of females or other males.

Seminal receptacles and spermatophores: morphology

Seminal receptacles are found in the genital segments of females, which run roughly from the 80th segment to the 100th segment. They are located dorsal and posterior to the nephridiopores, near the intersegmental junctions (Figs. 2, 3). Seminal receptacles are paired, blind, sac-like organs embedded in the body wall (Fig. 4). Each sac is about 40 μm long, and possesses a single 6 μm wide opening to the exterior. The wall of the sac is composed of columnar cells, except at the blind end where cuboidal cells predominate (Fig. 5). Some sacs are branched into two to four lobes (Fig. 6), and the number of lobes varies among and within females.

Each spermatophore is mushroom shaped, with a stalk and a spherical portion (Figs. 7, 8) containing sperm. Heads of individual spermatophores are about 40 μm in diameter, with the stalk about 135 μm in length. The spherical heads are covered by two layers, the outer characterized by a granular appearance, and the inner one with symmetrically arranged bands (Fig. 9a–c). Not every spermatophore produced is equipped with both layers, some occasionally lacking the outer layer (see arrows in Fig. 7). The sperm from broken spermatophores are morphologically identical to mature sperm seen in the coeloms of males (Fig. 10; also see Fig. 20c in Hsieh, 1984).

Transfer of spermatophores

Although the direct release of spermatophores from male gonoducts was not observed, expulsion of spermatophores from the tube openings of males was observed several times. When spermatophores were placed around the tube openings of female worms, these females—usually within one minute—would extend their anterior body portions out of the tubes, searching. Upon locating the spermatophores, they would pick them up with their first pair of parapodia and ventral palps, and then immediately withdraw to their tubes. In one instance, some spermatophores were literally carried out of a female's tube by larvae when the female and larvae were disturbed by routine observations. Upon examination under SEM, these spermatophores did not contain the outer granular layer (see Fig. 9c), suggesting that fe-

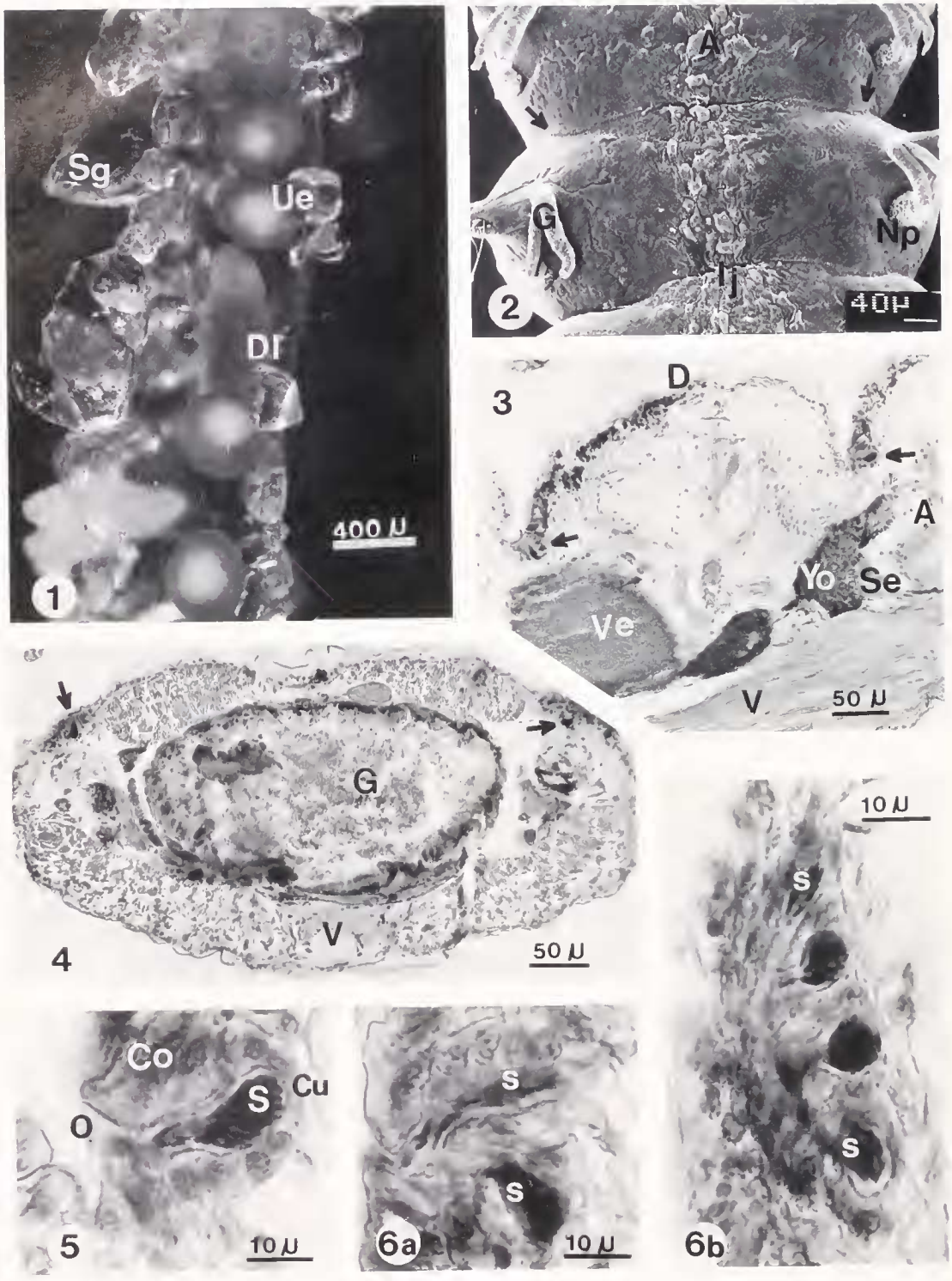


Figure 1. Unfertilized eggs and a developing embryo within a tube of *Kinbergonuphis simoni*. Dl = developing larva with 5 setigers; Ue = unfertilized eggs; Sg = sand grains.

Figure 2. Dorsal view (SEM) of a female *Kinbergonuphis simoni* showing the relative positions of seminal receptacles (arrows), nephridiopores (Np) and intersegmental junctions (lj). A = anterior end of the worm; G = gill.

males might manipulate spermatophores and mechanically break down the layers.

Fertilization efficiency

Fifty-one broods and 982 spawned eggs were examined. Out of 982 eggs, only 11 were unfertilized; this represents a fertilization efficiency of 98.9%.

Discussion

Sperm transfer in *Kinbergonuphis simoni* involves spermatophores and seminal receptacles. The seminal receptacles are embedded in the dorsal body wall, with external openings close to the nephridiopores. The nephridiopores serve as gonopores, while the adults' tubes serve as brood chambers. A similar spatial arrangement has also been found in the spionids (Söderström, 1920; Simon, 1967; Rice, 1987a), in the serpulids *Spirorbis spirorbis* (L.) (Daly, 1978), and in the capitellids (Eckelbarger and Grassle, 1987). A comparable situation also occurs in the galeommatacean bivalve *Mysella tumida*, where eggs are spawned, sperm are stored, and young are brooded in the same place: the suprabranchial chamber (Ó Foighil, 1985). The close proximity between openings of the sperm storage organs, gonoducts and brood chambers leads to a high fertilization efficiency. Efficiency has been shown to be 98.9% in *K. simoni* (this study), 98.8% in *S. spirorbis* (Daly, 1978), 100% in *Capitella* (Eckelbarger and Grassle, 1987), and 99.9% in a galeommatacean bivalve (Ó Foighil, 1985).

In *Kinbergonuphis simoni* the production of spermatophores can occur in the absence of females, and the release of eggs also can occur without the presence of males. Such phenomena have also been observed in spionids (S. Rice, University of Tampa, pers. comm.). Moreover, in *K. simoni*, *Polydora ligni*, and *Pseudopolydora paucibranchiata* (Myohara, 1980), females isolated from males can continuously produce viable offspring until the stored sperm are depleted. Two cases in *K. simoni* (Hsieh, unpub. data) also showed that, after their male mates had died, each remaining female (isolated from other males) continued to produce 4 more viable broods over periods of 30 to 40 days. These features reveal that sperm release and egg laying can take place separately, and that sperm are stored alive until needed. Thus, the pressure of breeding synchrony required in broadcast spawning is relieved. Consequently, asynchronous, prolonged, or even continuous reproduction can take place in the population over time. This prediction is consistent with the breeding pattern found in the field (Hsieh and Simon, unpub. data). Asynchrony and extended breeding may have advantages since the risk of reproductive failure can be spread over several reproductive events, and the chance that at least some offspring survive is higher (Stearns, 1976).

Sperm loss due to dilution by seawater has been assessed experimentally in broadcast spawning sea urchins (Pennington, 1985). With successful spermatophore transfer, females are provided with sperm packed in such a localized dense form that sperm dilution does not occur. Furthermore, in *Kinbergonuphis simoni*, spermatophores can remain intact for one to two days after being released into seawater. The reduction of sperm loss may be one of the advantages of having spermatophores.

The morphology of spermatophores in polychaetes is varied and species specific (*e.g.*, in the spionids, Richards, 1970; Greve, 1974; Rice, 1978a; and in an onuphid, this study). Despite the morphological differences, the method of spermatophore transfer in polychaetes appears similar. Spermatophores are released from the male tubes and subsequently are picked up by females. As proposed by Rice (1978a), this demonstrates that individuals do not have to leave their tubes or burrows for sperm transfer, and implies that the risks of being exposed to predation or disturbance are minimized when compared to other alternatives (*e.g.*, copulation, pseudocopulation, or indirect hypodermic impregnation).

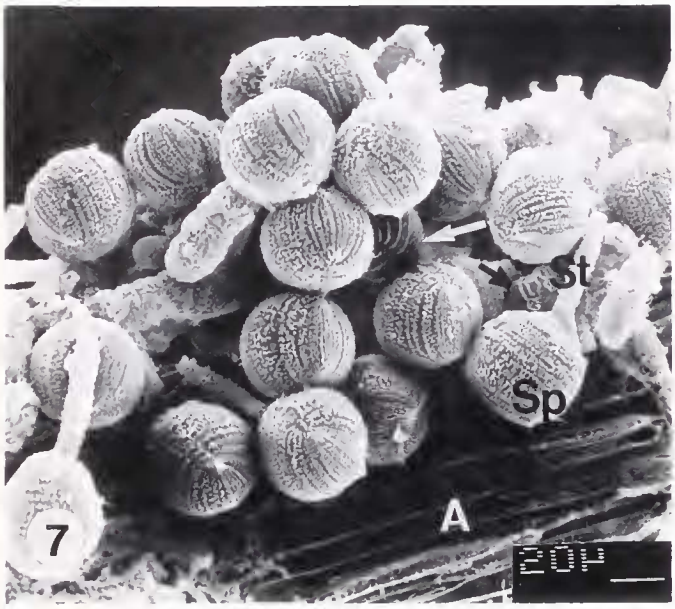
Table II summarizes the modes of sperm transfer known in polychaetes. Both the spionids and the onuphid have seminal receptacles in females, and spermatophores in males, for free transfer. In both families, worms are tube dwellers, tend to aggregate, and have similar life histories, suggesting similar selective pressures. In the Onuphidae, the predominant developmental pattern is lecithotrophic. Small-sized onuphids brood

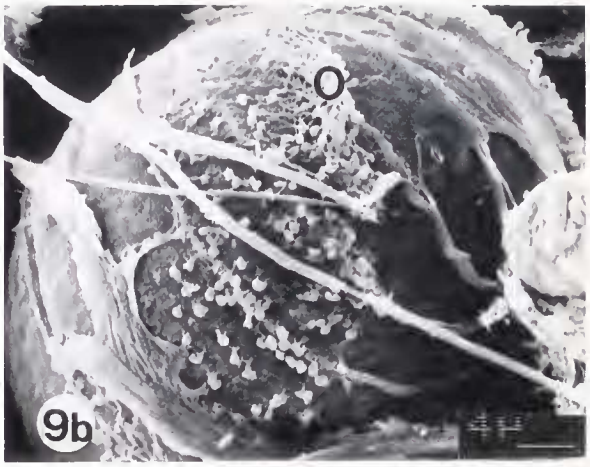
Figure 3. Sagittal section of a female *Kinbergonuphis simoni* showing the position of seminal receptacles (arrows). A = anterior end of the worm; D = dorsal; V = ventral; Ve = vitellogenic egg; Se = septa; Yo = young oocytes.

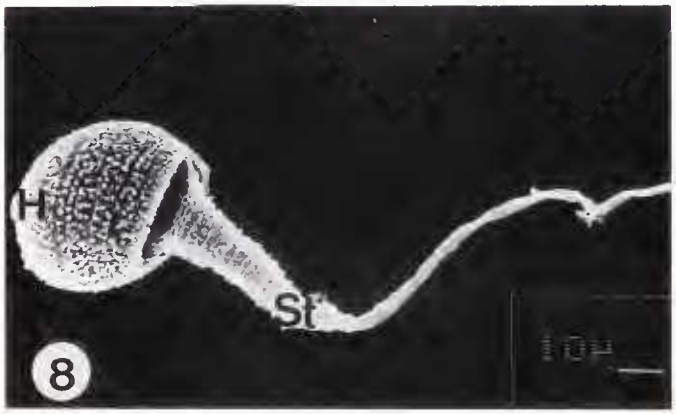
Figure 4. Cross section of a female *Kinbergonuphis simoni* showing paired seminal receptacles (arrows). G = gut; V = ventral nerve cord.

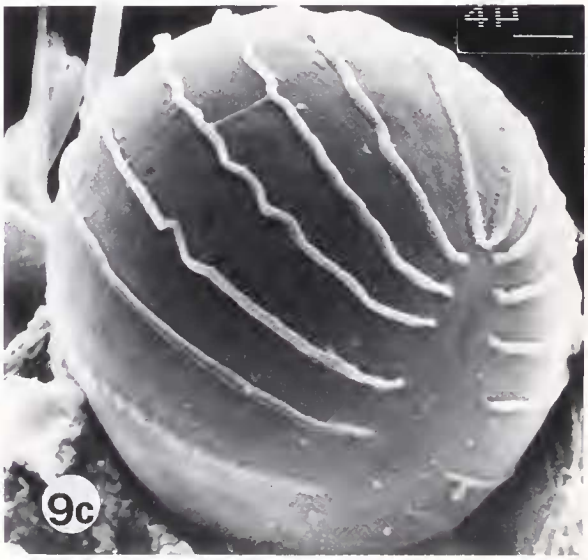
Figure 5. Individual seminal receptacle in female *Kinbergonuphis simoni* showing stored sperm (S). Co = columnar cell; Cu = cuboidal cell; O = opening of seminal receptacle.

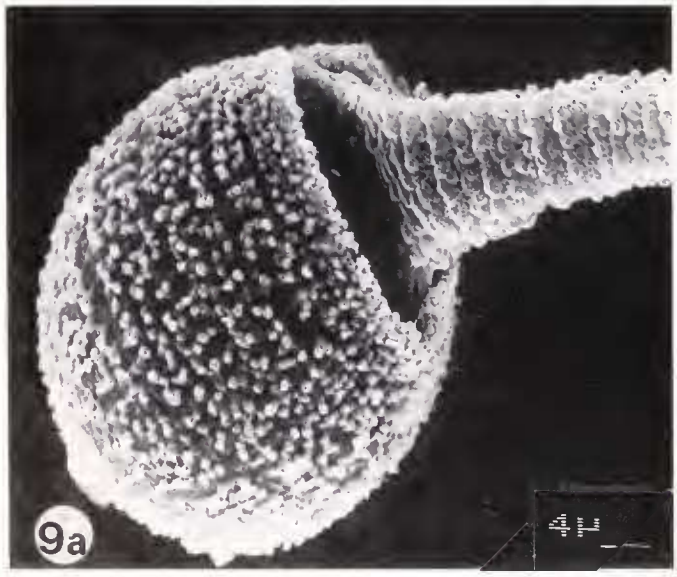
Figure 6. Branched seminal receptacles in female *Kinbergonuphis simoni*. (a) Bi-lobed. (b) Four-lobed. S = stored sperm.











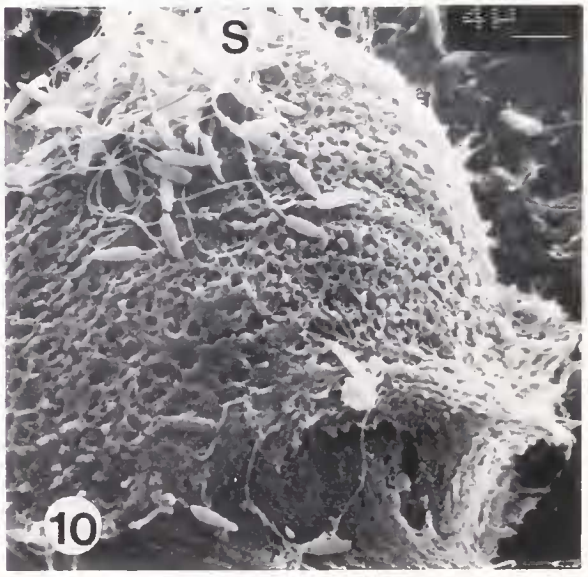


Figure 7. A clump of spermatophores produced by a male *Kinbergonuphis simoni*. A = a piece of ground alfafa; Sp = individual spermatophore; St = stalk of spermatophore; Arrows = spermatophores without outer layers.

Table II

Summary of sperm transfer modes in polychaete Families

Family	Adult life	Mode of sperm transfer	Reference
A) Non-aggregate transfer			
Nereidae Eunicidae Syllidae	Benthic motile forms	Broadcast spawning, mature individuals undergo swarming spawning with epitoke or stolon formation	Clark, 1961; Schroeder and Hermans, 1975
Pisonidae Saccocirridae	Interstitial forms	Copulation, females have seminal receptacles, males have copulatory organs	Gray, 1969; Westheide, 1984
Nereidae Polynoidae Phyllodocidae	Benthic motile forms	Pseudocopulation with pair formation or aggregations	Reish, 1957; Daly, 1973; Pettibone, 1963
B) Aggregate transfer			
Dinophilidae Protodrilidae Hesionidae	Interstitial forms	Hypodermic impregnation associated with spermatophores, seminal receptacles are present	Ax, 1968; Jouin, 1970; Westheide, 1984, 1988
Arenicolidae	Benthic burrowers	Free spermatophore transfer, the presence of seminal receptacles is unknown	Okuda, 1946
Spionidae	Benthic tube dwellers	Free spermatophore transfer, seminal receptacles are present	Söderström, 1920; Simon, 1967; Rice, 1978a, 1987a
Onuphidae	Benthic tube dwellers	Free spermatophore transfer, seminal receptacles are present	This study
C) Sperm transfer modes uncertain			
Alciopidae	Pelagic forms	Copulation or hypodermic impregnation has been suggested; naked sperm masses are embedded in epidermis; seminal receptacles are present	Pettibone, 1963; Rice, 1987b; Rice and Eckelbarger, 1989
Syllidae	Benthic motile forms	Copulation has been suggested; spermatophore-like structures are present in seminal receptacles	Goodrich, 1930
Terebellidae	Benthic tube dwellers	Pseudocopulation with pair formation or free transfer of aggregated sperm has been suggested; males become errant during spawning period; sperm morulae and free sperm are produced; the presence of seminal receptacles is unknown	Eckelbarger, 1974
Pectinariidae	Benthic tube dwellers	Free transfer of aggregated sperm has been suggested; sperm packets (spermatozeugmata) are produced; the presence of seminal receptacles is unknown	Austin, 1963, 1965
Capitellidae	Benthic burrowers or tube dwellers	Copulation, pseudocopulation or free spermatophore transfer has been suggested; seminal receptacles are present	Hartman, 1947; Reish, 1974; Eckelbarger and Grassle, 1987
Serpulidae Sabellidae	Benthic tube dwellers	Free spermatophore transfer has been suggested; seminal receptacles are present	Daly and Golding, 1977; Picard, 1980

larvae in maternal tubes (Fauchald, 1983; Hsieh and Simon, 1987). These reproductive characteristics lead us to predict that the sperm transfer mode seen in *Kinbergonuphis simoni* and spionids may commonly operate in other small onuphids as well. This proposal may also extend to other tube dwelling or burrowing polychaetes, if they share similar characters with onuphids and spionids in their life histories. Certainly, extensive studies covering tube dwellers and burrowers from different taxa are needed to test this hypothesis.

Most spionid spermatophores are morphologically adapted for flotation or enhanced suspension in the water (Rice, 1978a). In contrast, spermatophores of *Kinbergonuphis simoni* are sticky and often deposited on the bottom of culture dishes, or tangled with objects such as detritus or food particles, suggesting that the dispersal

Figure 8. Individual spermatophore of *Kinbergonuphis simoni*. H = head portion; St = stalk.

Figure 9. Covering layers of spermatophores in *Kinbergonuphis simoni*. (a) Outer layer with granular appearance. (b) Inner layer exposed after the outer layer being partially eroded. O = outer layer. (c) Inner layer showing symmetrical bands.

Figure 10. A broken spermatophore of *Kinbergonuphis simoni* showing escaped sperm (S).

ability of spermatophores is low. As a result, the exchange of spermatophores between individuals in distant populations is greatly reduced. Any changes in the timing of release, quantity and quality of spermatophores, or in the processes of spermatophore transfer and sperm storage, may alter the efficiency of fertilization. In turn, different methods of fertilization can serve as a barrier between populations and act as a reproductive isolation mechanism. In *K. simoni,* preliminary analyses of isoenzymes and morphometric measurements of populations from Tampa Bay, Ft. Myers, and the Indian River indicate that these populations differ (K. Fauchald, Smithsonian Institution, pers. comm.), suggesting that some form of divergence has taken place. Comparative studies of sperm transfer modes and sperm storage mechanisms among distantly distributed populations would be useful.

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